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Age and growth of the squid *Abraliopsis pfefferi* (Oegopsida: Enoploteuthidae) from the Central-East Atlantic based on statolith microstructure*

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SUMMARY: Statolith microstructure was studied in 29 specimens of the small micronectonic enoploteuthid squid *Abraliopsis pfefferi* (20-33 mm mantle length) captured in the open waters of the western part of the Gulf of Guinea in September 1988. Growth increments in statoliths were well-resolved and grouped into three almost translucent growth zones that could be distinguished mainly by increment width. Assuming growth increments as daily, as in other squids studied, males of *A. pfefferi* mature at ages ca 120-130 d, whereas females live up to 150-160 d. During its mature ontogenetic phase, *A. pfefferi* grow slowly (0.5-0.6% of mantle length per day). The main features of the life style in comparison with other squids are small adult sizes, *fast maturity rates* and two-three recruitments during one year.

Key words: statolith, age, growth, *Abraliopsis pfefferi*, squid.

RESUMEN: EDAD Y CRECIMIENTO DEL CALAMAR *ABRALIOPSIS PFEFFERI* (EOGOPSIDA: ENOPLOTEUTHIDAE) DEL ATLÁNTICO CENTRO ORIENTAL, A PARTIR DE LA MICROSTRUCTURA DE LOS ESTATOLITOS. – Se estudia la microstructura de los estatolitos de 29 especímenes del calamar enoplotéutido micronectónico *Abraliopsis pfefferi* (20-33 mm de longitud del manto), capturados en mar abierto en la parte occidental del golfo de Guinea, en septiembre de 1988. Los incrementos de crecimiento de los estatolitos se pudieron identificar bien y se agruparon de acuerdo con tres zonas de crecimiento cuasi-translúcidas que se pueden distinguir, principalmente, por la anchura del incremento. Asumiendo que los incrementos de crecimiento sean diarios, como en otros calamares, los machos de *A. pfefferi* maduran a la edad de 120 a 130 dias, mientras que las hembras tienen una longevidad de 150-160 dias. Durante su fase de madurez, *A. pfefferi* crece lentamente (0.5-0.6% diario de longitud del manto). Las principales características de la biología de esta especie, comparada con la de otros calamares, son el pequeño tamaño de los adultos, las altas tasas de madurez, y el hecho de tener de dos a tres reclutamientos anuales. (Translated by the Editor)

Palabras clave: estatolitos, edad, crecimiento, *Abraliopsis pfefferi*, calamares.

INTRODUCTION

Abraliopsis pfefferi, Joubin, 1896 is an abundant inhabitant of the tropical and subtropical Atlantic, the Gulf of Mexico and Mediterranean Sea (Nesis, 1987). Like most of the enoploteuthids of the subfamily Enoploteuthinae, *A. pfefferi* is a small-sized squid attaining maximum mantle lengths of 42 mm (Clarke, 1966). Together with other abundant enoploteuthid species of the genera *Abralia*, *Abraliopsis*, *Pyroteuthis* and *Pterygioteuthis*; *A. pfefferi* is a member of a micronectonic teuthofauna that plays an important role both in epipelagic and mesopelagic trophic webs of the open Atlantic. Little is known about its biology. In the tropical Atlantic, juveniles were captured in epipelagic layers near the frontal zone of the South Trade Current and subtro-

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pical waters (Arkhipkin and Schetinnikov, 1989). Maturing and mature adults of *A. pfefferi* were encountered mainly in subtropical waters, occurring in the mesopelagic layers during day and ascending into epipelagic waters at night (Murzov, 1986). Age and growth of *A. pfefferi* remain unknown.

Until now, age and growth of enoploteuthid squids have been studied using either length-frequency analysis (*Watasenia scintillans* from the Japan Sea, Hayashi, 1993) or statolith ageing techniques (*Abraliopsis atlantica* and *Enoploteuthis leptura* from the tropical Atlantic, Arkhipkin and Murzov, 1990, Arkhipkin, 1994; *Abralia trigonura* from the North Pacific, Young and Mangold, 1994). For the latter species, growth increments were validated to be daily by keeping newly hatched paralarvae in aquaria and subsequently comparing the growth increment number within their statoliths with the number of days elapsed from hatching to death (Bigelow, 1992). Growth increments within *A. trigonura* statoliths started depositing outside the nucleus just after hatching (Bigelow, 1992). It has been revealed that the life span of both fast-growing *E. leptura* and slow-growing *A. atlantica* and *A. trigonura* is about 6 months (Arkhipkin and Murzov, 1990, Bigelow, 1992, Arkhipkin, 1994), while *W. scintillans* (Hayashi, 1993) exhibits a 12 month life cycle.

The purpose of this paper is to assess the age and growth of *A. pfefferi* by statolith microstructure studies and to compare them with those of other enoploteuthid species.

MATERIALS AND METHODS

Twenty-nine *A. pfefferi* of 20-33 mm ML (21 females and 8 males) were captured during the biological surveys on the orange-back squid *Sthenoteuthis pteropus* (Ommastrephidae) in the central-east Atlantic by R/V *'Ocher'* in September 1988. Sampling localities covered open waters of the western part of the Gulf of Guinea (latitudes 2°15'N-3°30'S and longitudes 4°05'-15°W) off the Exclusive Economic Zones of African countries. Squids were caught at night (20:00 p.m.- 04:00 a.m) at depths of 25-300 m using the Russian zoological pelagic trawl RT/TM 33 type (vertical opening 8-10 m) equipped with a 6 mm mesh liner. Immediately after capture, *A. pfefferi* were identified by the key elaborated by Nesis (1987). The dorsal mantle length was measured to the nearest 1 mm, body weight to the nearest 0.1 g. Maturity stages were assigned from the scale developed for ommastrephid squids (Zuev et al., 1985).

Statoliths were extracted from the statocysts of squid aboard ship and stored in 96% ethanol until further analysis at the Laboratory of Commercial Invertebrates of AtlantNIRO using statolith-ageing techniques (Arkhipkin, 1991). Before grinding, the total statolith length was measured after Clarke (1978). From each pair, only one statolith was ground first anterior side, then posterior side on a wet waterproof sandpaper (1000 grit), polished on a fine sandpaper (1500 grit) and embedded in Canada balsam. Growth increments were examined and counted from the nucleus to the edge of the dorsal dome by two observers using the eye-piece micrometer of a 'Biolam-R14' light microscope (magnification x400) (Arkhipkin, 1991) . Total number of growth increments for each specimen was obtained as an average of count numbers if deviation between the average and counts was less than 5%.

Growth increments within statoliths of *A. pfefferi* were well-resolved, unambiguous and similar in appearance and microstructure to daily growth increments of the similar species *A. trigonura* (Bigelow, 1992). Assuming them to be daily, the total number of growth increments in the ground statolith of *A. pfefferi* was assumed to represent the age of the squid in days. Hatching dates were back-calculated. Age-at-length and age-at-weight data were fitted with either linear or power functions using the linear regression and method of iterative nonlinear least squares, respectively. Instantaneous growth rates (G) were calculated after Forsythe and Van Heukelem (1987):

$$G = (\ln W2 - \ln W1)/T,$$

where W1 and W2 are either mantle length (mm) or body weight (g) at the beginning and end of time interval (T = 10 days).

RESULTS

Statolith microstructure and growth

Growth increments were revealed in all ground statoliths (Fig. 1). They started depositing outside an ovoid nucleus. The diameter of the nucleus varied from 18 to 22 um. Maximum width of growth increments was observed in the dorsal dome.

Growth increments formed three main growth zones which could be distinguished mainly by incre-

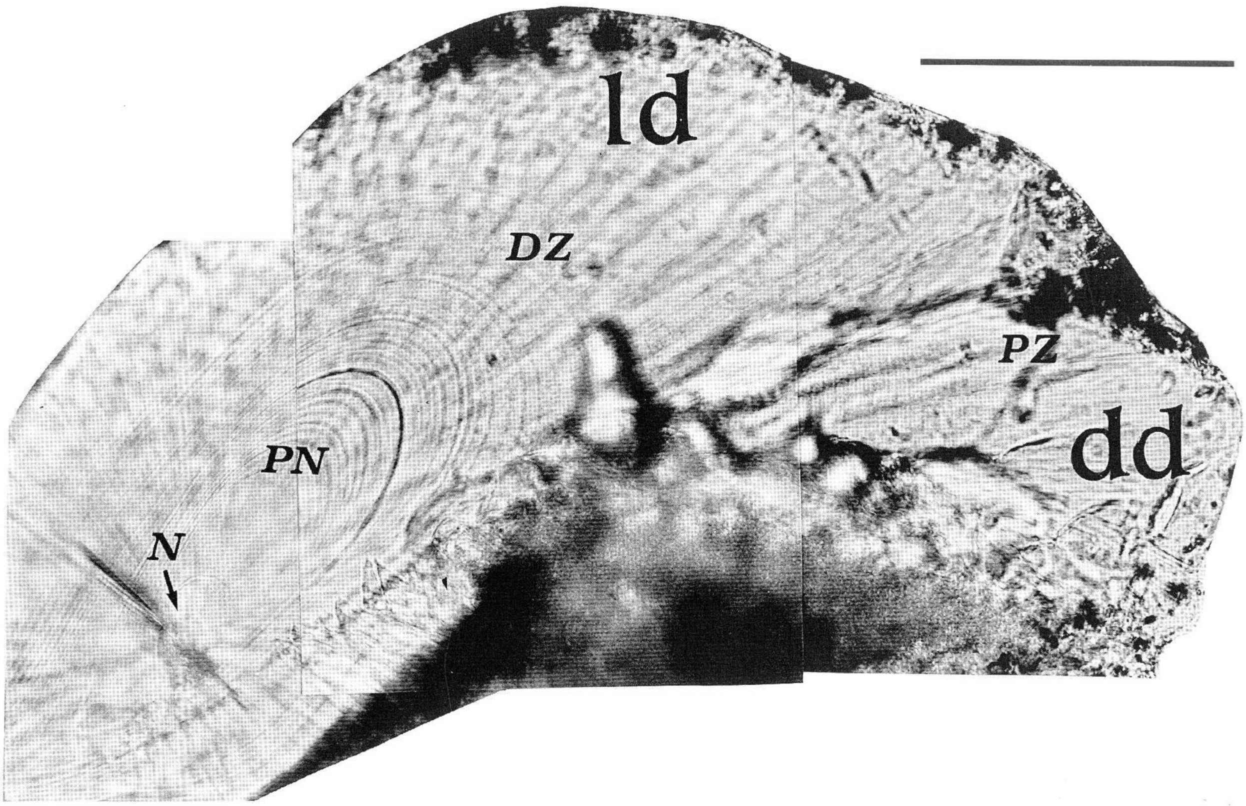

FIG. 1. – *Abraliopsis pfefferi*. Compound light microphotograph of statolith of maturing male (ML 78 mm). Nucleus (N), postnuclear zone (PN), dark zone (DZ) and peripheral zone (PZ) in the lateral (ld) and dorsal (dd) domes of the statolith. Scale bar = 100 um.

ment width. In different statoliths, colour of all zones varied from translucent to slightly brownish in transmitted light of the microscope. There were no distinct boundaries between growth zones, or pronounced checks. A total number of growth increments in the postnuclear zone was 20-25 (mean 22.3) with a mean width being ca 6 um. The 'dark zone' (which in this species was not really dark like in ommastrephids) consisted of 24-32 (mean 26.5) growth increments with a mean width of increments of 4-5 um. The peripheral zone was distinguished from the 'dark zone' mainly by sharply decreasing width of growth increments (up to 1.8-2.2 um).

For the size range studied (ML 20-33 mm), statoliths of *A. pfefferi* are relatively large, and the total statolith length (STL) differs significantly for both sexes. Males have relatively larger statoliths (mean 2.438% ML, sd = 0.2485) than the same-size females (mean 1.987% ML, sd = 0.1699). Allometric growth of the total statolith length (STL) versus ML was negative (Fig. 2A).

The relationship between the total number of growth increments in statoliths and STL was approximated by a linear function. In contrast to the allometric growth of statoliths, sex dependent differences in absolute growth were not revealed (Fig. 2B).

Age and growth of squid

In our samples, minimum age (86 d) was observed both in a maturing male of 22 mm ML and a maturing female of 24 mm ML. Maximum age was revealed in a mature male of 25 mm ML (127 d) and in a mature female of 33 mm ML (154 days) (Fig. 2C).

Due to the shortage of data available, it was impossible to construct growth curves for males and females separately. Length-at-age data pooled for both sexes were best described by a linear function, whereas pooled weight-at-age data were best described by a power function (Fig. 2 C,D). However, it is evident that *A. pfefferi* has sexually dimorphic growth both in length and weight: male points are plotted mainly below the growth curves, whereas those of females are above it (Fig. 2 C,D). This sexually dimorphic growth begins at an age of 90-

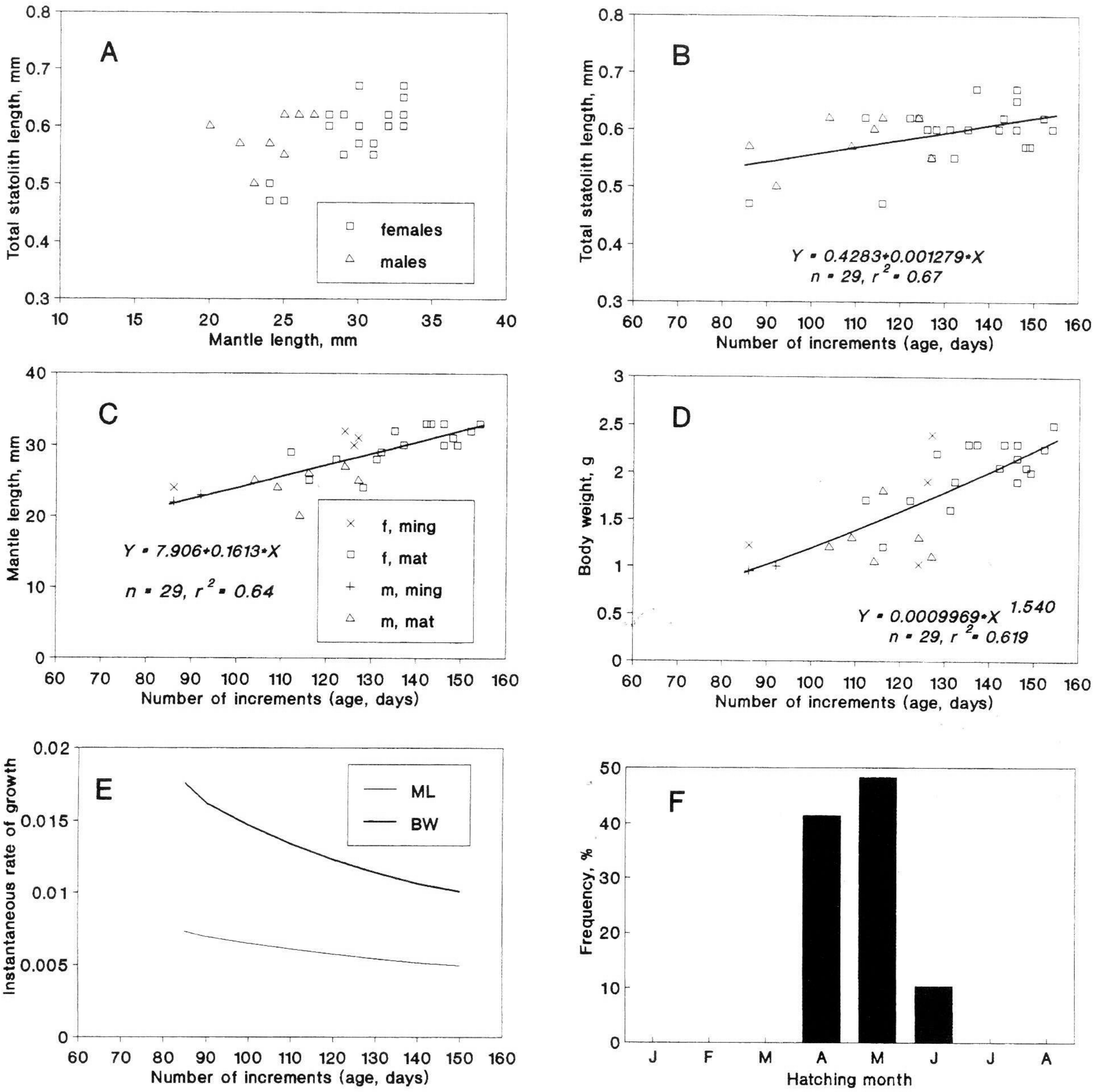

FIG. 2. – *Abraliopsis pfefferi*. Relationships between: (A) mantle length and total statolith length, (B) number of increments in statoliths and statolith length, (C) number of increments and mantle length, (D) number of increments and body weight, (E) number of increments and instantaneous rate of growth in mantle length and body weight, (F) hatching dates.

100 d. Owing to this, males achieve 25-27 mm ML and 1.2-1.6 g BW by the age of 120-125 d. At the same age, females are 29-30 mm ML and 1.8-2 g BW. It is notable that there were no males older than 127 d in our samples, whereas many mature females had an age of 130-150 d.

A. pfefferi is a rather slow-growing squid during its adult stage. G of ML decreases from 0.0073 at age of 85 d to 0.005 at age 150 d, G of BW falls more sharply, from 0.0176 to 0.0101, respectively (Fig. 2E).

Maturation and hatching dates

In our samples, there were only maturing and mature animals (Fig. 2 C). All squids of ages < 100 d were maturing. Minimum age of the mature males was 105 d, that of mature females 113 d. All males older than 105 d were mature (V maturity stage) and remained in this condition until an age of 125-127 d. In contrast, some females which had an age of 122-127 d and close to the maximum ML (30-32 mm) were still maturing. All females older than 127 d were mature until an age of 152-154 d. Almost all mature females (except two specimens of 25 and 27 mm ML) had copulated. Regarding the group growth curves, both sexes continue growing with low growth rates at mature stage (Fig. 2 C,D).

Hatching dates fell mainly in April and May with a low proportion of June-hatched squid (Fig. 2F).

DISCUSSION

It is hard to find any differences in statolith shape of both *A. pfefferi* (Fig. 1A) and *A. atlantica* adults (Arkhipkin and Murzov, 1990). However, the inner structure of the statoliths of both species has some specific characters. Maximum diameter of the nucleus of *A. pfefferi* (ca 20 um) is somewhat larger than those of *A. atlantica* (12 um) and *Abralia trigonura* (12.7 um) (Arkhipkin and Murzov, 1990, Bigelow, 1992). For the latter species it has been revealed that the nucleus is in fact the statolith of newly hatched paralarva (Bigelow, 1992). Taking into account the larger egg size in *A. pfefferi* (0.95x1.3 mm) than in *A. atlantica* (0.75x1.0 mm) (V.V. Laptikhovsky, AtlantNIRO, pers.comm.) and *A. trigonura* (0.72x0.92) (Young and Harman, 1985), it is reasonable to expect larger *A. pfefferi* hatchlings and correspondingly larger statoliths (= nuclei).

The practically translucent inner structure of the statoliths seems to be a characteristic feature for the squids of the subfamily Enoploteuthinae. In *E. leptura* and *A. atlantica*, the medium 'dark' growth zone has a slightly brownish colour almost like the postnuclear and peripheral zones (Arkhipkin and Murzov, 1990, Arkhipkin, 1994). In *A. trigonura* (Bigelow, 1992) and *A. pfefferi*, all zones are translucent. Thus, growth zones can be distinguished mainly by increment width. Usually it is possible to distinguish the postnuclear and medium zones by slightly broader growth increments in the postnuclear zone. Absence of a prominent stress mark situated on the boundary between the postnuclear and medium zones in *A. pfefferi* and the other enoploteuthids studied perhaps derives from the fact that their food capture apparatus does not transform during paralarval and juvenile phases (Clarke, 1966). Such a stress mark appears between the postnuclear and dark zones of statoliths in ommastrephids during transformation from rhynchoteuthion into juvenile (Arkhipkin and Mikheev, 1992). At that time their food capture apparatus changes, causing a short-term starvation and corresponding decrease of statolith growth.

The total number of growth increments in the postnuclear zone (mean 22.3) is higher than in *A. atlantica* (12) and *E.leptura* (19). Bigelow (1992) did not distinguish postnuclear and dark zones in A. trigonura statoliths. However, a sum of the total numbers of growth increments in both zones (41-48.8) is very similar in all enoploteuthids studied. Calculated ML at this age ranges from 10.9 in *A. trigonura* to 12 mm in *A. atlantica* and 15 mm in *E.leptura*. Until this age, all species of enoploteuthids studied are juveniles, occurring continually in the superficial warm water layer. Juveniles > 12-15 mm ML start their vertical migrations, ascending to the surface layers at night and plunging into mesopelagic waters during the daytime (Arkhipkin and Schetinnikov, 1989). Thus, the hypothesis of Arkhipkin and Murzov (1990) and Bigelow (1992) of a sharp decrease of statolith growth rates (= formation of the peripheral zone with very narrow growth increments) during transition from holoepipelagic (paralarvae and early juveniles) to nictoepipelagic (late juveniles and adults) life styles seems to be similar for all enoploteuthid species.

A. pfefferi is a short-lived animal. Taking into account the age of specimens with maximum-known ML (32-33 mm and 25-27 mm in females and males, respectively), males of *A. pfefferi* mature and perhaps, die after copulation at ages around 4 months, whereas females live up to 5-5.5 months. Maturation in both sexes starts about 20 d later than in *A. atlantica* (Arkhipkin and Murzov, 1990) mainly due to specific or ambient temperature differences for both species. In the Gulf of Guinea, *A. atlantica* lives mainly in warmer waters of the South Trade Current, whereas *A. pfefferi* prefers colder waters of the northern part of the South Subtropical Gyre (Arkhipkin and Schetinnikov, 1989). It seems that *A. pfefferi* has slower growth rates than *A. atlantica* for the same reason.

It is considered that squids of the family Enoploteuthidae are multiple spawners releasing individual eggs in epipelagic waters (Young and Harman, 1985, Young et al., 1993). Females of *A. pfefferi* become mature, copulate at age ca 4 months and have a possibility to spawn until age of 5-5.5 months. Development of eggs has to be rather fast (ca 10-12 d) due to their small sizes and high ambient temperatures (Laptikhovsky, 1991). Thus, the life span (including time of egg development) of *A. pfefferi* may vary from 4 to 6 months resulting in production of two-three generations per year.

Small sizes with rapid maturation and several recruitments per year enable *A. pfefferi* to utilize effectively resources of the trophic levels of the oceanic epipelagia and to keep a high abundance of its populations in the open waters of the Gulf of Guinea.

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